PREDATORS, PATCHES IN SPACE AND TIME AND THE INFLUENCE OF HABITAT COMPLEXITY ON THEIR INTERACTIONS

By

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

1996

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by

To my father

ACKNOWLEDGMENTS

Funding for this project was provided by the Institute of Food and Agricultural Sciences at the University of Florida, Archbold Biological Station, and a private donation by Frank "Sonny" Williamson. Archbold Biological Station provided housing, laboratory space, and use of a four-wheel drive vehicle. The cooperation of the staff at Archbold Biological Station and the MacArthur Agro-Ecology Research Station is greatly appreciated.

I thank my committee members, Lyn Branch, Dick Franz, Carmine Lanciani, and Carole McIvor for their help and support throughout my project. I chose my committee members with specific purpose in mind, hoping that their differing specialties would provide a broad and balanced assessment of my work. They fulfilled that purpose. I particularly want to thank George Tanner for serving as my advisor. George provided a supportive base from which to work. His easy-going nature made working on a complicated project relatively painless.

Natalie Hardman was hired as an assistant during my first sampling season. She had a strong desire to learn about amphibians. Unfortunately, the weather did not

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I want to thank my family for their support In particular, I want to thank my parents and grandparents for introducing me to the great outdoors and encouraging my interest in nature. Finally, I want to thank Leslie whose support and friendship over the past thirteen years has made all of this possible

This is contribution No 26 from the MacArthur Agroecology Research Center.

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Comparis[illegible], sample compos[illegible]
1994 and [illegible]ner breeding sea[illegible]
that were [illegible]rd were not (n 5) [illegible]
flooding [illegible]tes containing [illegible]
Species co[illegible]d as temporary s[illegible]
were spectm[illegible]al do not breed in [illegible]
predators [illegible]ylio, Rana utri[illegible]
gryllus, and [illegible] cinerea will bre[illegible]
predators and [illegible] categorized as [illegible]
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1 Variation in water depth (mean +1 [illegible]
sampling dates (top), wetland (mi[illegible]
wetland zone (bottom). Zone means w[illegible]
letters are significantly different [illegible]

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wetland zone (bottom). [illegible]

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(top), wetland (middle), and wetland zone
(bottom). Zone means with different letters are
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letters are significantly different [illegible]

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letters are significantly different. [illegible]

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and age at metamorphosis (bottom). Squares indi[illegible]
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Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

TADPOLES AND PREDATORS: PATTERNS IN SPACE AND TIME AND THE INFLUENCE OF HABITAT COMPLEXITY ON THEIR INTERACTIONS

By

Kimberly Jane Babbitt

August, 1996

Chairman: George W. Tanner
Major Department: Wildlife Ecology and Conservation

I examined the spatial and temporal dynamics of tadpoles and aquatic insect predators in 12 temporary wetlands in south-central Florida. I also conducted experiments on the role of habitat structural complexity in mediating predator-prey interactions. Eleven species of anurans bred in the wetland sites; Rana utricularia accounted for 44% of all captures. Species diversity was positively correlated with wetland size but was unrelated to hydroperiod. Varied meteorological conditions, coupled with the presence of a system of drainage ditches, resulted in annual variation in hydrologic conditions that had a lasting effect on species composition. Flooding resulted in the intrusion of water from ditches that contained fish into otherwise isolated wetlands. Species that breed exclusively

n site within [illegible] disturbance resulted a system that i both spatia temporally dynamic resulting in variable assemblage structure and composition at affected sites. Distrib patterns of tadpoles within wetlands were related wit habitat features. Both tadpole and aquatic insect pred numbers varied among wetlands and across time, but w distributed relatively evenly within wetlands. Thus selection for microhabitat at the within-wetland scale d not appear to be strong. Distribution patterns of tadpoles appear to be more strongly related to macrohabitat selecti of breeding sites by adults than by microhabitat selection within wetland sites. Experiments demonstrated that increased cover can reduce predation rates by aquatic insects on tadpoles that reduce activity in response to predators (R. utricularia), and those that do not (Hyla squirella). Thus, although distribution patterns in the field were not correlated strongly to habitat features, tadpole success still may be influenced strongly by them. Finally, reductions in activity in response to predators had growth and developmental costs in R. utricularia that were dependent on background resource level. Tadpoles on low food metamorphosed at later dates but at larger sizes when exposed to predators. Tadpoles on high food also had prolonged development but were smaller compared to tadpoles not exposed. Thus, assessment of responses to both resource

level and threat of predation may be necessary for understanding the consequences of cost-benefit trade-offs mediated by behavior

CHAPTER 1
INTRODUCTION

Overview

One of the major goals in ecology is to determine the [illegible] influence patterns of distribution and [illegible] of species. This task is not a simple one because [illegible] factors impinge upon the ecological and evolutionary [illegible] that result in observed relationships among [illegible] Resource availability, the distribution of plant [illegible] to a many spatial and temporal scales, and the biotic [illegible] tions among species change similarly. The resulting [illegible] eous environment offers choices to the organisms [illegible] t. How an individual responds to habitat [illegible] ty may influence food availability and predation [illegible] nisms can have important influence on [illegible] dynamics and ultimately evolutionary processes [illegible]

[illegible] of the factors influencing distribution [illegible] y animals is complicated by their comple [illegible] which include a terrestrial adult stage and an [illegible] life (Wilbur 1980). Examinations of habitat [illegible] attributing of aquatic assemblages have [illegible] the adult (Fowler and Bowler 1978, Toft 1980). Analyses

of larval assemblages usually address temporal partitioning
[illegible] n and Heyer 1968, Wells 1981) or partitioning relative
[illegible] permanent versus temporary pond sites (Gascon 1991,
[illegible] 1991). Most authors come to similar conclusions
[illegible] habitat partitioning of larval assemblages
[illegible] ources are partitioned along spatial (temporary versus
[illegible] r pond) and temporal (breeding season) axes. Less
[illegible] has been done on larval food partitioning; however,
[illegible] suggests that partitioning along the food axis is
[illegible] as that along temporal and spatial axes
[illegible] all (Fauth 1986, Heyer 1974, 1976, Seale and
[illegible]).

[illegible] s will provide important information regarding
[illegible] ion pressures relative to habitat use and
[illegible] partitioning (Crump 1984, Magnusson and Hero 1991).
[illegible] provide a complete picture of the
[illegible] l [illegible] of tadpoles because they focus on one scale
[illegible] [illegible] of organisms can be examined on a
[illegible] [illegible] [illegible] [illegible] [illegible] [illegible]
[illegible] [illegible] factors that can influence tadpole
[illegible] as competitor or predator abundance and
[illegible] ity in space to oviposit among wetland sites
[illegible] (Smith 1983, Wells and McAleer 1994, Woodward
[illegible] [illegible] pulations within wetlands (Alford
[illegible] Wiehl 1988, 1990). Therefore, the distribution
[illegible] f tadpoles at both the microhabitat (feeding

[illegible] aid at [illegible] nonabitat (patch site) scale can have a large [illegible] [illegible] [illegible] growth and survival and thereby [illegible] [illegible] structure

[illegible] [illegible] importance of considering scale has been [illegible] [illegible] (Wiens 1989, 1992). Few studies of tadpole [illegible] [illegible] have addressed this issue. Processes that are [illegible] important population regulatory factors at one scale of [illegible] [illegible] may not operate at other scales (Wiens [illegible] [illegible]). For example, predation has been identified as an [illegible] [illegible] influencing anuran breeding site selection [illegible] (Magnuson [illegible] [illegible]). However, how predators affect tadpoles [illegible] [illegible] [illegible]

lish predators dominate in permanent sites; however, systems that have a cycle of filling and drying prevent predatory fish populations from becoming established. A switch from [illegible] to invertebrate or salamander-dominated predator systems occurs along the gradient so that tadpoles developing in temporary and ephemeral sites are subject to a different suite of predators.

Because biotic and abiotic conditions change along a hydroperiod gradient, tadpoles developing in different habitats face a different set of challenges. Traits that promote developmental success at one end of the hydrologic gradient may not be suitable at the other end. For example, [illegible] alteration in anti-predator mechanisms in response to [illegible] in predator regimes in bromeliad habitats (Acevedo-Ramos et al. 1998, Babbitt et al. 1998, Woodward 1983). The larvae of several species typical breed in permanent sites are palatable to fish whereas species that breed in ephemeral sites without fish do not possess this anti-predator mechanism (Formanowicz and Brodie 1982, Kats et al. 1988). In addition, [illegible] activity, are often absent in species that breed in [illegible] sites (but see [illegible]).

Decreased foraging activity may reduce growth or [illegible] (Werner and Anholt 1993, and Werner [illegible]). At the [illegible] affect [illegible] from predator [illegible] other [illegible] this at from habitat

[illegible] (Newman 1987, Rowe and Dunson 1993, 1995). Thus [illegible] behavioral traits for reducing predation risk), while [illegible] in permanent habitats can lead to increased [illegible] in ephemeral sites.

The trade-off between rapid development and anti-predator responses appears to be a major factor limiting the distribution of anurans to certain types of breeding sites (Heyer, Werner and McDiarmid 1991). Weak anti-predator [illegible] may increase developmental rates in ephemeral [illegible] will result in mortality in permanent sites (Heyer 1994; Woodward 1983). As a broad generalization [illegible] tend to breed in permanent sites are passively excluded [illegible] by brief developmental periods [illegible] that breed in ephemeral sites are excluded [illegible] by predation.

[illegible] Within [illegible] habitats [illegible] distribution patterns [illegible] (1) [illegible] [illegible] [illegible]

found in the inner non-vegetated zones. Although most species occurred in several of the vegetated zones, significant differences in spatial distribution were detected. Three species were most abundant in the shallow zone, two species were most abundant in the emergent zone and one species was most common in the submergent zone.

Larval assemblages also may separate along thermal (Heyer and Pyburn 1983, Pechmann 1985) and water column (Heyer 1973, Pechmann 1985) gradients. Ontogenetic changes in microhabitat use also have been found relative to size class in Rana sphenocephala. Alford and Crump (1981) found significant intraspecific (between size class) and interspecific spatial partitioning among four anuran species in a single temporary pond site. Two species, Pseudacris crucifer and Pseudacris ornata, separated relative to cover, temperature, and their responses to these features changed over time. Alford (1986) suggested that these responses were probably largely due to competitive avoidance behavior between size classes. However, he did not examine the potential influence of predators.

Differences in predator abundance or composition also may exist within a single pond. Although pond size and the relative abundance of predators may be important factors in the tadpole-predator system, they do not account for spatial segregation between predators and prey to be an important

assembla

Predation, Habitat Structure, and Behavior

[illegible] can be a significant regulating factor [illegible] (reviewed by Gilliam et al. 1989). A potential [illegible] is assemblages have shown that differential [illegible] competitively dominant [illegible] [illegible] conditions of low (Morris et al. 1984, Werner et al. 1983a) [illegible] competitive ability is [illegible] to [illegible] [illegible] [illegible] to [illegible] [illegible] [illegible]

...1983). Considering the important effect predators have ... tadpole survival and assemblage ... little ... has focused ... how habitat structure affects ... interactions. More ... that ... suggested that Pseudacris ... tadpoles survive ... by ... but ... vulnerability to ... of litter. In contrast ... live ... foraged ... the water column. Whether differences in ... activity ... for ... important in determining vulnerability ... has ...

... of the few ... have ... the ... are observed in clarity, little ... But ... to ... the ... of tadpoles ... ...

examination of the distribution patterns of larvae and predators at 4 spatial scales (microhabitat, habitat, wetland core, and within core) across 4 summer and 1 winter breeding seasons; (2) experimental manipulations to determine the effect of microhabitat on predation, and (3) laboratory observations on the effects of predation on growth and development under controlled conditions.

I examined spatial and temporal distribution patterns of [illegible] to determine whether [illegible] were consistent with [illegible] and Wilbur's Habitat Templet [illegible] at different scales. [illegible] processes [illegible] the [illegible] required [illegible] of the [illegible] [illegible] [illegible]

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the jopin frog (Rana

study. This species

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ferles [illegible]

[illegible]

[illegible]

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tudy hydroperiods varied almost by a factor of five (1 e
to 263 days) Hydroperiods in the curre t study varied by
ly a factor of 1 4, from 49 to (weeks Further the
hydroperiod of these wetlands was m h lo r t than the
inimum required for metamorphosis of all the anuran species
i ng at MARC (Ellis 1961 Will 1971 l v y t
tudy, Dodd (1992) did not find a relationsh p between
abitat duration and species r ches at a simile temporary
wetland in north central Florida That study was conducted
ring a drought, and visitat rly al l amphibians was not
ecessarily assoc ated with breeding activity Large
fferences in hydrology among (((((years) may be
required to generate significant differences in species
ss Relevant differences ma not be sig with
hydroperiods that are too short for some species to
successfully produce metamorph ((((with
fish predators It is likely that the wetlands the
tudy v (((((

community member
studies provide
particular clinic
towards with relat
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Table 2.1 Occurrence and abundance* of tadpoles at 12 temporary wetlands at MAERC

	Wetland												
	1	2	3	4	5	6	7	8	9	10	11	12	Total
Bufo quercicus	0	0	0	14	0	0	0	0	0	0	0	19	33
Hyla gratiosa	1	0	1	2	0	0	0	2	15	11	2	9	43
Acris gryllus	0	0	5	10	61	8	23	51	1	5	2	25	191
Hyla squirella	81	173	60	26	1	168	3	6	20	48	48	0	634
Hyla cinerea	52	12	7	0	0	0	3	1	14	18	22	0	129
Hyla femoralis	0	0	0	129	73	1	3	0	0	0	0	20	224
Pseudacris nigrita	0	0	0	0	0	44	10	0	0	0	0	0	54
Pseudacris ocularis	0	1	2	21	43	105	99	17	0	5	1	18	313
Gastrophryne carolinensis	16	73	12	0	0	0	4	[illegible]	6	1	26	0	139
Rana grylio	7	7	[illegible]	6	216	0	2	5	1	17	0	40	303
Rana sphenocephala	398	160	35	42	39	19	319	348	68	[illegible]	101	22	1604
Unidentified Hyla	1	0	0	1	1	0	0	0	0	8	0		11
Total	554	426	123	300	432	345	401	433	126	170	202	153	3678

*Number of individuals captured in a 1.95m traps combined within each wetland

Figure 2-1 Map of the MacArthur Agro Ecology Research Center showing the system of ditches that enhance drainage

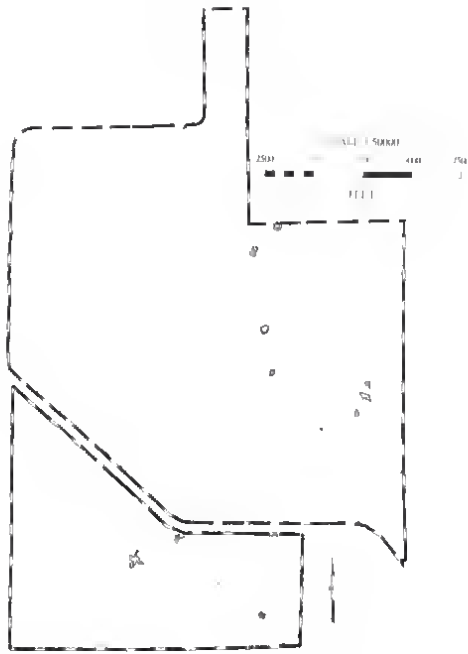


Figure 2.2- Location of wetland study sites at MAERL

Figure 2-3 Abundance of tadpoles of anuran species at 12 temporary wetlands at MAERC. Bars are mean ± 1 SE and are based on total combined captures in all 0.25m traps at each wetland.

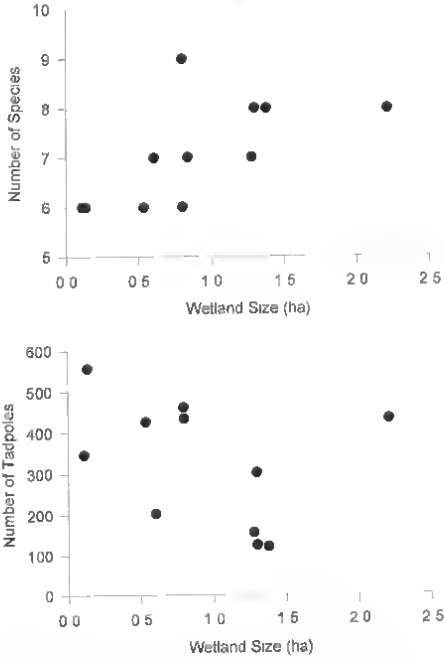


Figure 2-4. Relationship between wetland size and anuran species richness (top) and abundance (bottom). Abundance and richness based on total captures from all 0.25m traps within each wetland.

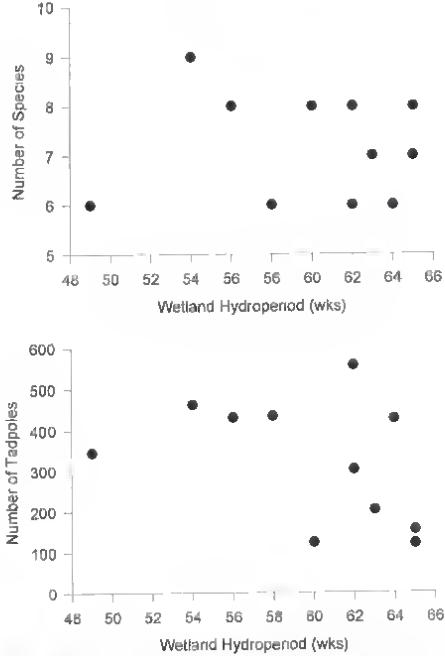
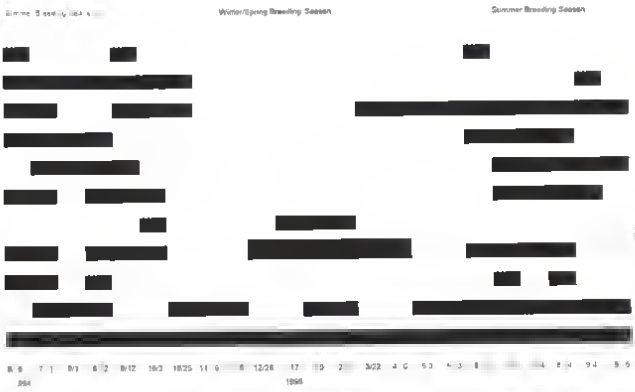
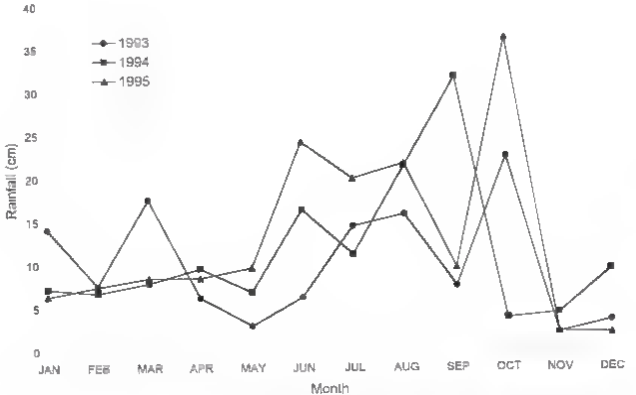


Figure 2. Relationship between wetland hydroperiod and anuran species richness (top) and abundance (bottom). Abundance and richness based on total captures from all 0.25m² traps within each wetland.


Winter/Spring Breeding Season
Summer Breeding Season
Bufo quercicus
Hyla gratiosa
Acris gryllus
Hyla squirella
Hyla cinerea
Hyla femoralis
Pseudacris crucifer
Pseudacris ocularis
Gastrophryne carolinensis
Rana grylio
Rana utricularia
1994
1995


1993
1994
1995
Rainfall (cm)
0
5
10
15
20
25
30
35
40
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
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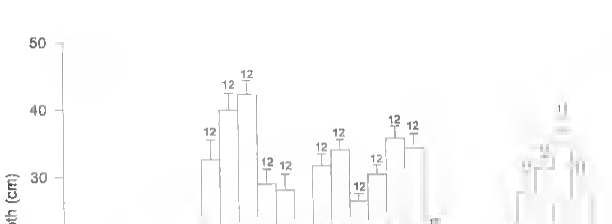
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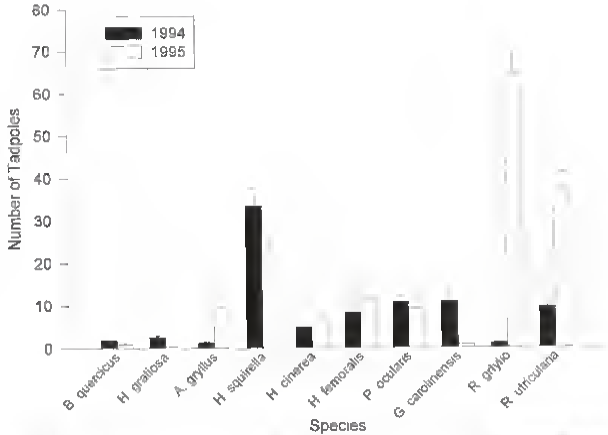

Figure 2-9. Comparison of mean (+ 1 SE) tadpole abundance at temporary pools in the summer breeding season (June-Sep emphasis during 1994 and 1995 the combined samples of all 0.25m traps at each period

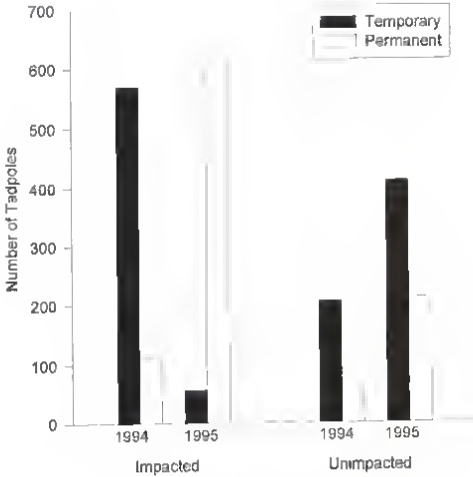

Figure 10. Comparison of total sample composition between the 1994 and 1995 summer breeding seasons at wetlands that were (n = 6) and were not (n = 6) impacted by flooding from beavers containing fish predators. Species categorized as temporary site breeders were species that do not breed in wetlands with fish predators. Rana grylio, Rana utricularia, Bufo quercicus, and Hyla cinerea will breed with fish present and were categorized as permanent site breeders.

CHAPTER 3
SPATIAL AND TEMPORAL DYNAMICS OF TADPOLES AND AQUATIC INSECT PREDATORS DEVELOPING IN TEMPORARY WETLANDS

Introduction

Predation is a major source of mortality in anuran tadpoles (Calef 1973; Heyer et al. 1975; Smith 1983), and is thought to have a large influence on breeding site selection by adult anurans (Magnusson and Hero 1991). Fish are major predators of tadpoles in permanent aquatic sites, and many species appear to avoid breeding in sites that contain fish predators (Hopey and Petranka 1994, Rosetarris and Wilbur 1991). Although ephemeral wetland sites generally do not contain fish predators, the short duration of these sites makes them unsuitable for species with long larval developmental periods (Wilbur 1980, 1984, 1987). Thus differences in habitat duration and predator composition coupled with interspecific differences in the selection of breeding sites by adults, can generate differences in species composition of larval anurans along gradients of habitat permanence (Werner and McPeek 1994).

However, factors that influence tadpole success, such as abundance and composition of competitors or predators, vary in space not only among wetland sites (Gascon 1992, Smith 1983; Werner and McPeek 1994, Woodward 1983) but also

among patches within wetlands (Banks and Beebee 1988, Diehl 1988, 1992). Therefore, the distribution patterns of tadpoles and predators at both the macrohabitat (breeding site) and microhabitat (patch site) scale can have a large influence on tadpole growth and survival, and thereby assemblage structure.

Although the importance of considering scale has been widely discussed (Wiens 1989, 1992), few studies of tadpole ecology have addressed this issue. Processes that are important in population regulation at one scale of investigation may fail to operate at other scales (Wiens 1989). For example, whereas predator composition has a large influence on anuran breeding site selection, the spatial dynamics of predators and tadpoles at the within-wetland scale are poorly understood. If tadpoles occupy patches that provide increased protection from predators, such as areas with high cover (Babbitt and Jordan 1996, Chapters 4 and 6), or areas with lower predator densities (Banks and Beebee 1988), then differential habitat use within sites may be an important feature influencing predation rates, and possibly assemblage structure (Morin 1986).

Spatial overlap at the within-wetland scale among tadpoles and predators may be high if both groups select microhabitats based on similar abiotic features such as water depth, temperature, or plant cover. Understanding such patterns and how they vary in space and time, should

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The goal of this study was to
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Sampling Methods

From May 1994 through September 1995, I sampled 12 wetlands every three weeks (n 23 sampling periods) One wetland was dropped during the last si sampling periods due to damage from cattle trampling At each site, I collected 9 samples using a stratified random sampling protocol Three replicate samples were collected in each of 3 concentric belts corresponding appro imately to one third the radius of the wetland

Tadpoles and macroinvertebrates were collected with a 1/4 m open-ended, bo trap Bo traps have been used to sample small fish and macroinvertebrates (Chick et al 1992; Freeman et al. 1984. Kushlan 1981) and anuran larvae (Caldwell et al 1980, Calef 1973 Pfenning 1990), and are effective for sampling in areas with comple vegetation structure A bar seine fitting the diameter of the bo trap and fitted with fiberglass insect screening was swept through the water column (after vegetation had been cleared) until 3 consecutive sweeps yielded no additional captures Samples were preserved in the field with 10% buffered formalin Macroinvertebrates were removed from formalin, rinsed thoroughly in water and stored in alcohol in the lab Tadpoles and macroinvertebrates were identified to species. For the purposes of this study, the macroinvertebrate assemblage was analyzed as a whole rather than by species The assemblage consisted of 11 species of odonates from the

residuals for the measures of environmental parameters indicated that transformations were not necessary (Sokal and Rolf 1981). The main effects of wetland and zone were tested over the split-plot error (i.e., wetland x zone), whereas the time and time x zone effects were tested over the whole plot error (i.e., mean square error). The Bonferonni-Dunn post hoc multiple comparisons tests was used to test for differences among the three zones when a significant ($p<0.05$) zone effect was detected (Day and Quinn 1989).

Correlation analyses were performed to examine the relationships between the abundance of all tadpoles combined, as well as the abundance of the three most common anurans (*H. squirella*, *R. utricularia*, and *P. ocularis*), with habitat variables and macroinvertebrate abundance and biomass (Sokal and Rolf 1981).

Results

Physical Parameters

Water depth, water temperature, pH, plant cover, and plant biomass all varied significantly among wetlands and across time (Table 3.1; Figures 3.1 through 3-5). The main effect of time, which reflects seasonal differences, accounted for most of the variation in water depth (37%) and water temperature (58%). In contrast, wetland explained a majority of the variation in pH (73%), plant cover (46%), and plant biomass (29%). Wetlands that were adjacent to

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number and many ships were very weak The ship was a negative More com e patterns emerge some stronge relationships were detected the three mo species are e amined separatel H squirella a negative relationship with wate depth and a relationship with temperature and pH (Table 3 addition H squirella was negatively correlate biomass R utricularia also had a negative rel with water depth but this relationship was weak to H squirella, R utricularia was negatively with temperature The differences between these reflect the interspecific differences in seasona breeding activity R utricularia also was po correlated with plant cover P ocularis number related partially with any of the variables measured

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Discussion

[redacted]s of tadpole abundance within wetland[redacted] e evidence that differential o upation wi[redacted] es was an important anti predator mechanism [redacted] fferences in tadpole abundance among wetland[redacted] atistically significant, these differences e[redacted] e percent of the total variation in tadpole numb[redacted] Examination of the entire tadpole assemblage as a group may obscure some species-specific patterns that may exist; however, separate analyses of the three most abundant ecies did not reveal any differences in distributior elative to wetland zone. Because predator numbers and biomass also were distributed relatively equally among zones, differential use by tadpoles presumably would not have been an effective mechanism for avoiding predators.

In addition to the lack of differences in distributior ted on wetland zone, tadpoles showed weak relationships ith habitat characteristics. Examination of the entire

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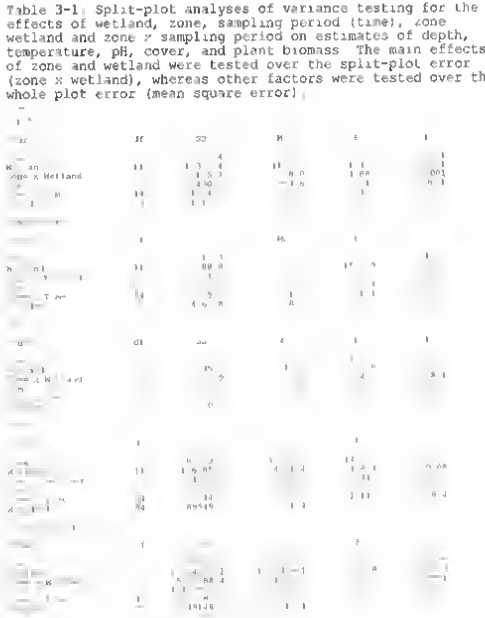
Table 3-1. Split-plot analyses of variance testing for the effects of wetland, zone, sampling period (time), zone wetland and zone x sampling period on estimates of depth, temperature, pH, cover, and plant biomass. The main effects of zone and wetland were tested over the split-plot error (zone x wetland), whereas other factors were tested over the whole plot error (mean square error).



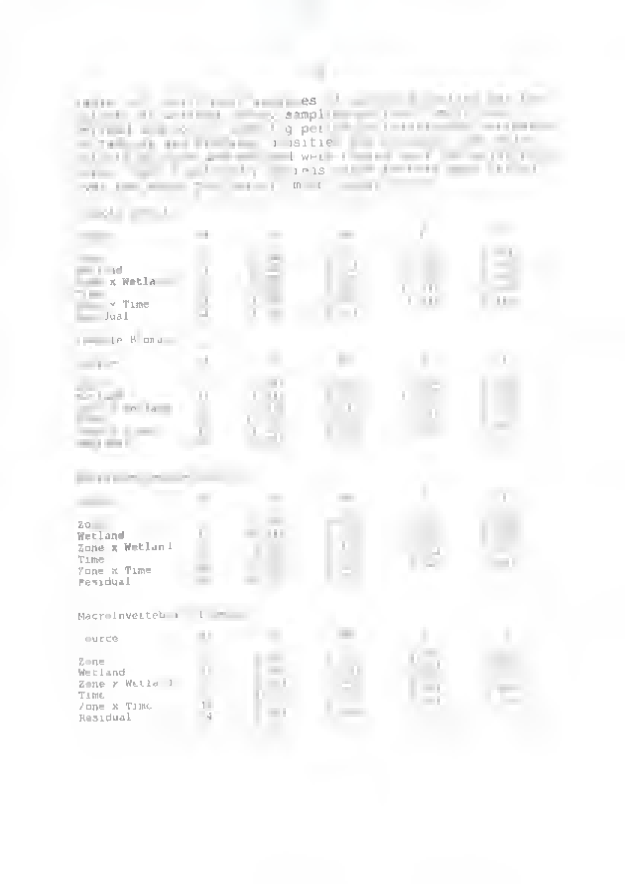


Table 3.3. Split plot analyses of variance testing for the effects of wetland, zone, sampling period (time), zone x wetland and zone x sampling period on transformed estimates of *H. squirella*, *R. utricularia*, and *P. ocularis* densities. The main effects of zone and wetland were tested over the split-plot error (zone x wetland), whereas other factors were tested over the whole plot error (mean square error).

H. squirella

Source	df	SS	MS	F	P
Zone	2	0.042	0.021	3.246	0.0582
Wetland	11	0.813	0.074	11.398	0.0001
Zone x Wetland	22	0.143	0.006	0.348	0.9978
Time	22	9.084	0.367	19.726	0.0001
Zone x Time	44	0.337	0.008	0.405	0.9998
Residual	594	11.065	0.019		

R. utricularia

Source	df	SS	MS	F	P
Zone	2	0.072	0.036	1.048	0.3743
Wetland	11	7.187	0.653	18.767	0.0001
Zone x Wetland	22	0.766	0.035	0.915	0.5746
Time	22	6.248	0.284	7.468	0.0001
Zone x Time	44	3.772	0.074	1.955	0.0003
Residual	594	22.592	0.038		

P. ocularis

Source	df	SS	MS	F	P
Zone	2	0.044	0.022	2.011	0.1578
Wetland	11	1.240	0.113	10.243	0.0001
Zone x Wetland	22	0.242	0.011	0.928	0.5581
Time	22	1.03	0.0	4.019	0.0001
Zone x Time	44	0.161	0.004	0.308	1.0000
Residual	594	7.047	0.012		

Table 3 4 Correlations between all species, Hyla squirella, Rana utricularia, and Pseudacris ocularis with water depth, temperature, pH, plant cover, total plant biomass, and macroinvertebrate density and biomass

		r	p
Water depth vs.	H. squirella	0.432	0.0008
	R. utricularia	-0.197	0.0020
	P. ocularis	-0.051	0.6752
	All species	-0.230	<0.0001
Temperature vs	H. squirella	0.391	0.0027
	R. utricularia	0.244	0.0002
	P. ocularis	0.152	0.2254
	All species	0.122	0.0017
pH vs	H. squirella	0.386	0.0030
	R. utricularia	0.150	0.0557
	P. ocularis	-0.181	0.1948
	All species	0.130	0.0025
Plant biomass vs.	H. squirella	-0.295	0.0257
	R. utricularia	0.014	0.8218
	P. ocularis	-0.026	0.8292
	All species	-0.069	0.0691
Plant cover vs.	H. squirella	0.132	0.3291
	R. utricularia	0.254	<0.0001
	P. ocularis	0.190	0.1155
	All species	0.151	0.0001
Macroinvertebrate density vs	H. squirella	0.269	0.0668
	R. utricularia	-0.035	0.6014
	P. ocularis	-0.073	0.6139
	All species	-0.073	0.0530
Macroinvertebrate biomass vs	H. squirella	-0.029	0.8477
	R. utricularia	-0.100	0.1344
	P. ocularis	0.245	0.0838
	All species	-0.136	0.0003

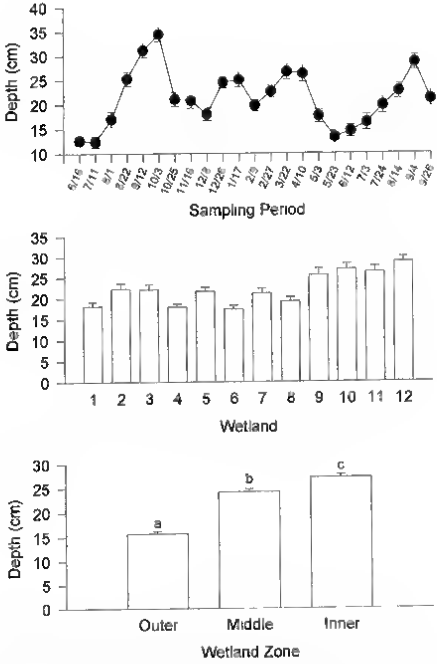


Figure 3-1 Variation in water depth (mean +1 SE) among sampling dates (top), wetland (middle), and wetland zone (bottom). Zone means with different letters are significantly different

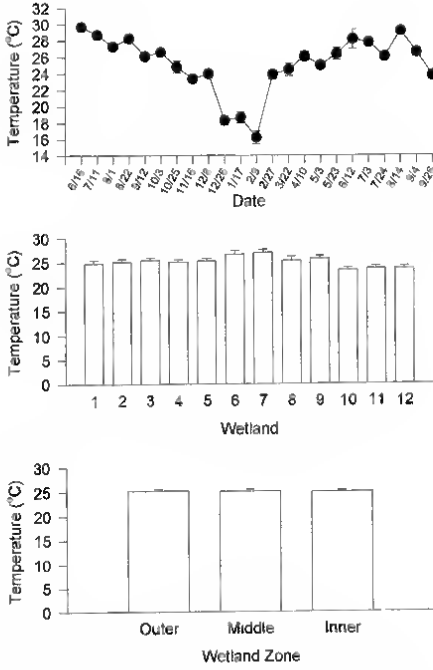


Figure 3-2 Variation in water temperature (mean +1 SE) among sampling dates (top), wetland (middle), and wetland zone (bottom).

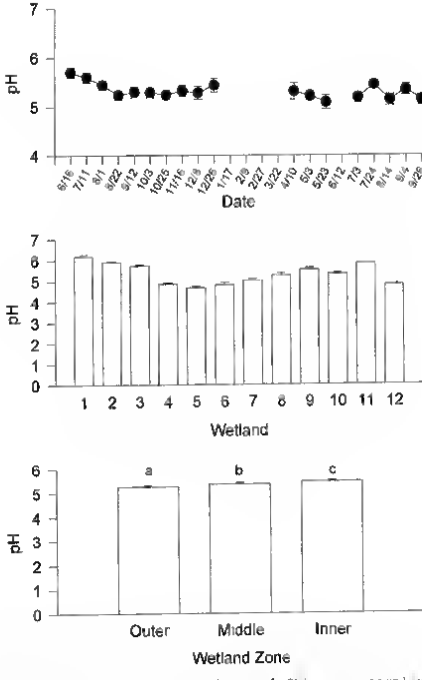


Figure 3-3 Variation in pH (mean ±1 SE) among sampling dates (top), wetland (middle), and wetland zone (bottom). Zone means with different letters are significantly different

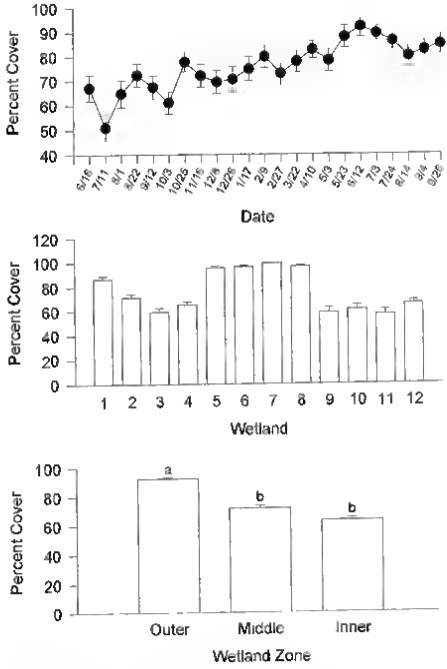


Figure 3-4 Variation in plant cover (mean +1 SE) among sampling dates (top), wetland (middle), and wetland zone (bottom) Zone means with different letters are significantly different.

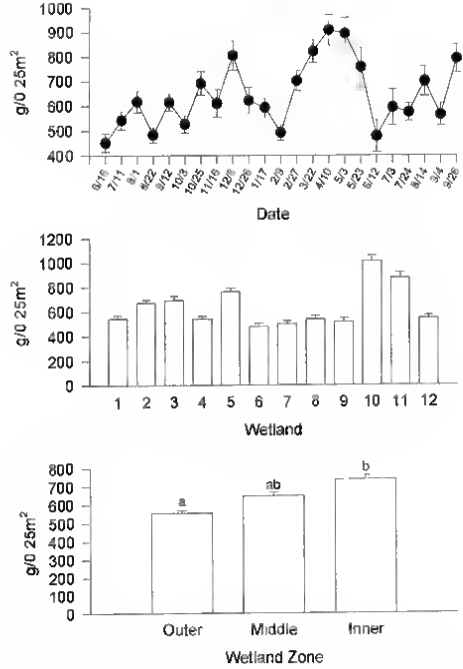


Figure 3-5. Variation in plant biomass (mean +1 SE) among sampling dates (top), wetland (middle), and wetland zone (bottom). Zone means with different letters are significantly different

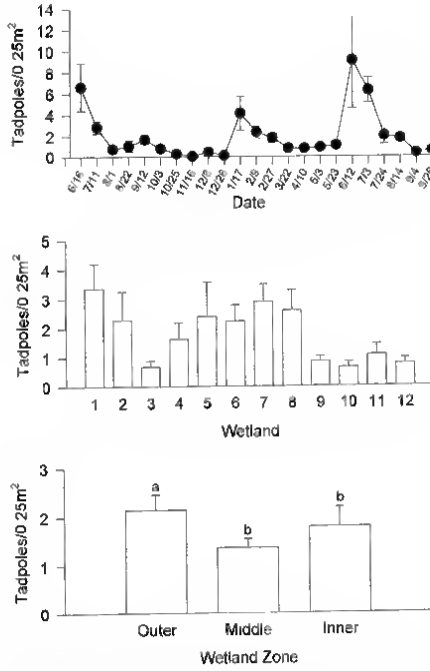


Figure 3.6 Variation in tadpole numbers (mean +1 SE) among sampling date (top), wetland (middle), and wetland zone (bottom). Zone means with different letters are significantly different

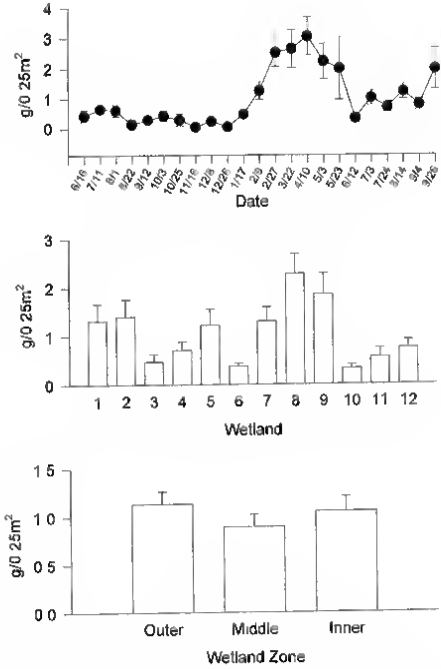


Figure 3-7. Variation in tadpole biomass (mean ±1 SE) among sampling date (top), wetland (middle), and wetland zone (bottom)

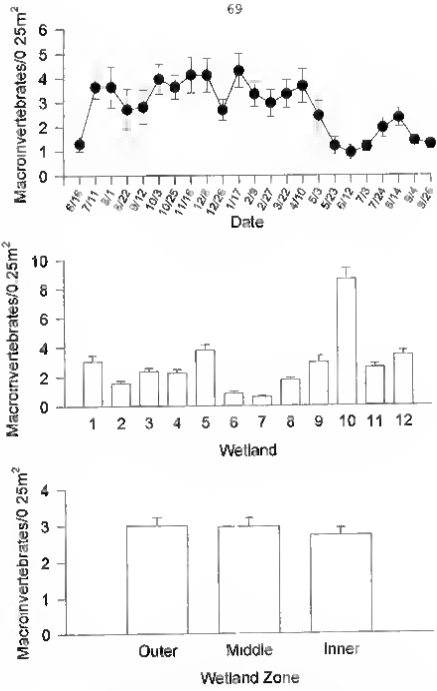


Figure 3-8. Variation in macroinvertebrate predator numbers (mean ± 1 SE) among sampling date (top), wetland (middle), and wetland zone (bottom).

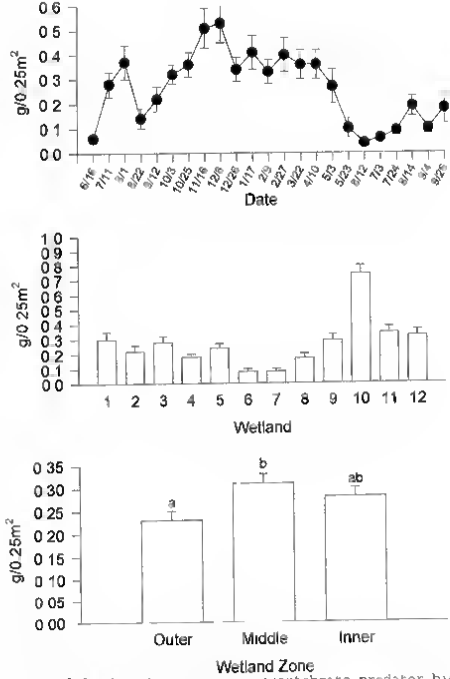


Figure 3-9. Variation in macroinvertebrate predator biomass (mean +1 SE) among sampling date (top), wetland (middle), and wetland zone (bottom). Zone means with different letters are significantly different.

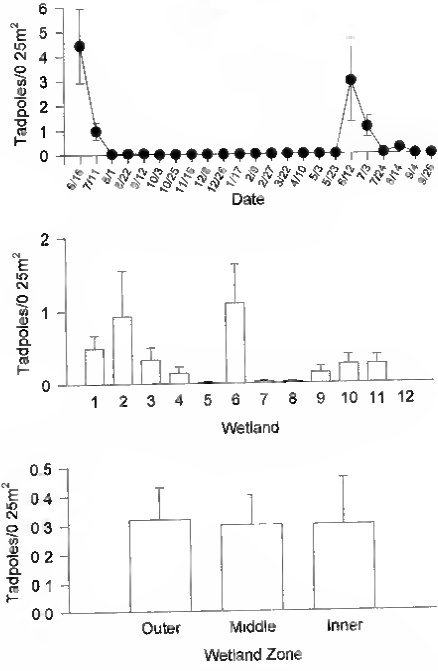
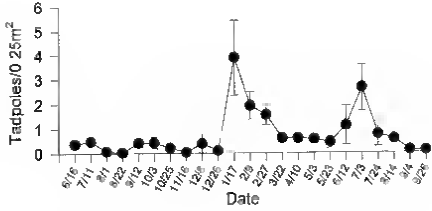
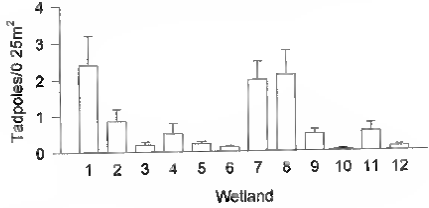


Figure 3-10: Variation in Hyla squirella numbers (mean +1 SE) among sampling date (top), wetland (middle), and wetland zone (bottom)





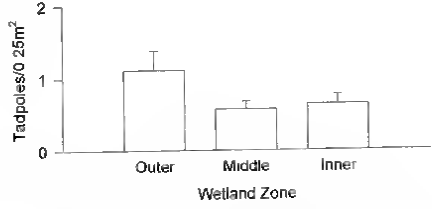


Figure 3-11 Variation in Rana utricularia numbers (mean +1 SE) among sampling date (top), wetland (middle), and wetland zone (bottom).

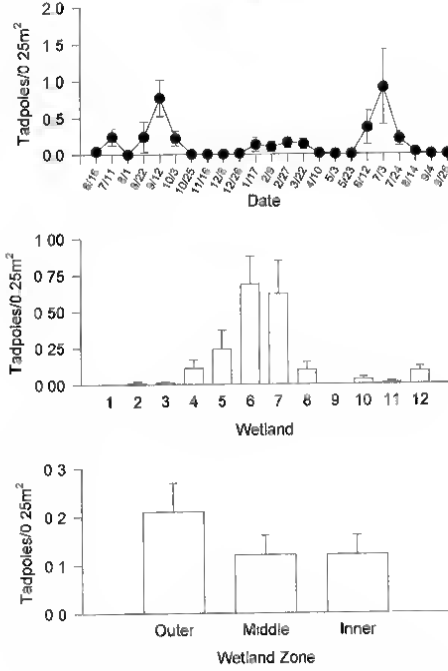


Figure 3-12. Variation in Pseudacris ocularis numbers (mean +1 SE) among sampling date (top), wetland (middle), and wetland zone (bottom)

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were analyzed using analysis of variance (ANOVA) for repeated measurements. Dependent One treatment was pool develop in tadpole [illegible] for [illegible] rogoral [illegible] effect of [illegible] and [illegible] [illegible] [illegible]

predator treatments Tadpole mass did not differ between the small predator and no predator treatments within the ow cover treatment (F 0 41), p 0 53)

Age at Metamorphosis

The main effect of predator and the interaction of predator and cover had a significant effect on age at metamorphosis, however, the main effect of cover was not significant (Figure 4-1; Table 4-1) At high cover levels, age at metamorphosis was not significantly affected by predator treatment (F-0 01, p 0 9-) However within the low cover treatment, tadpoles e posed to large predators metamorphosed earlier (F-11;34, p 0;001) compared to the small and no predator treatments, which did not differ (F-0 001, p=0 97)

Discussion

Predator size had a much larger effect on tadpole performance than did level of habitat comple ity High cover level did reduce predation levels compared to low cover when large predators were present, suggesting that habitat comple ity does provide increased protection from predators The most parsimonious interpretation for ta k of effects by small predators is that tadpoles were able to grow large enough early in the e periment to reach a size refuge and escape predation Thus, early growth by R utricularia

habit

tadpole

Table 4.1 Summary of ANOVA for responses of Rana utricularia tadpoles to cover and predator treatments. CD is the coefficient of determination, which is the percentage of variation in the response variable attributable to the treatment effect.

Percent Survival

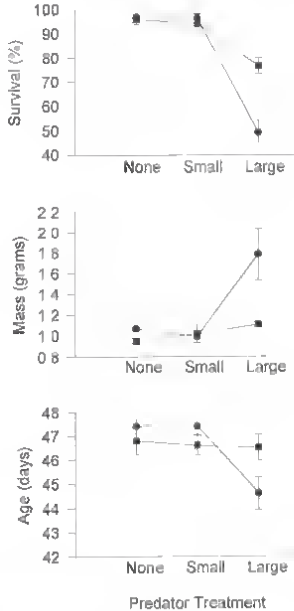
Source of variation	df		F	P	CD
Block	3	0.03844	0.68	0.578	2.3
Predator	1	1.74807	31.92	0.001	71.6
Cover	1	0.07293	1.86	0.194	3.1
Predator × Cover	1	0.13464	3.77	0.051	8.3
Error	14	0.12271			

Mass (g)

Source of variation	df	SS	F	P	CD
Block	3	0.01849	1.47	0.165	7.6
Predator	1	0.10171	16.40	0.001	42
Cover	1	0.03519	11.11	0.005	14.3
Predator × Cover	1	0.011	4	0.008	17.4
Error	14	0.044			

Age (days)

Source of variation	df		F	P	CD
Block	4	0.0004	0.0	0.83	5
Predator	1	0.00088	4.04	0.041	24
Cover	1	0.0001	0.41	0.450	1.4
Predator × Cover	1	0.00107	4.89	0.025	29.4
Error	11	0.01151			



[illegible] 1 Mean (± 1 SE) responses of [illegible] to fever and predator treatments [illegible] (top), wt to [illegible] at metamorphosis (middle) [illegible] metamorphosis (bottom). Squares indicate high [illegible] rate low [illegible]

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invertebrate, prey movement is an important component of predator detection (Lima and Dill 1990). Therefore, the costs of reduced activity in terms of prolonged larval period should be weighed against the benefit of decreased predation risk. Because R. utricularia breeds in temporary sites, it would be instructive to test the response of tadpoles to the presence of predators under varying drying regimes to determine whether R. utricularia can balance the costs and benefits of foraging versus predator detection with the costs of habitat drying.

Reductions in size at metamorphosis can have potential costs regardless of breeding habitat association. Size at metamorphosis can have an important influence on adult survival and reproductive fitness (Berven 1990, Goater 1994, Semlitsch et al. 1988, Smith 1987). In this study, tadpoles on the higher plane of resources that responded to predators incurred relatively higher cost in terms of reduced size at metamorphosis, although they had absolutely larger masses compared to tadpoles on the lower food treatment. Food treatment had a greater effect on growth than did predator treatment. Increased size at metamorphosis as a response to increased food has been documented numerous times (reviewed in Wilbur 1980). That food availability had such a large effect on growth is not surprising; however, the differential costs of responding to predators on different food treatments is. These results demonstrate the need for

Table 5-1: Summary of ANOVA for growth and larval period responses of *Rana utricularia* tadpoles to food and predator treatments. CD is the coefficient of determination, which is the percentage of variation in the response variable attributable to the treatment effect.

Mass (mg)

Source of variation	df	SS	F	P	CD
Block	5	0.0309	2.10	0.1221	1.67
Food	1	0.0904	30.74	0.0001	48.97
Predator	1	0.0012	0.42	0.5248	0.65
Predator . Food	1	0.0180	6.12	0.0259	9.75
Error	15	0.0441			

Larval period (days)

Source of variation	df	SS	F	P	CD
Block	5	0.0008	1.01	0.4064	3.24
Food	1	0.0192	130.28	<0.0001	77.73
Predator	1	0.0021	13.97	0.0020	8.50
Predator . Food	1	0.0004	2.50	0.1344	1.62
Error	15	0.0022			

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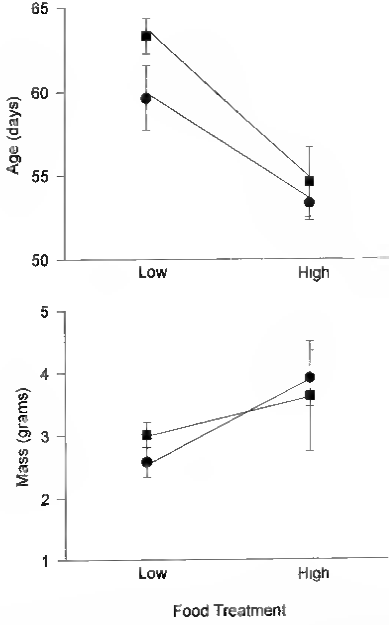

Figure 5-1. Mean (± 1 SD) responses of Rana utricularia tadpoles to food level and predator treatments: age at metamorphosis (top) and wet mass at metamorphosis (bottom). Circles indicate predator absent and squares indicate predator present. (n=6 for all treatments)

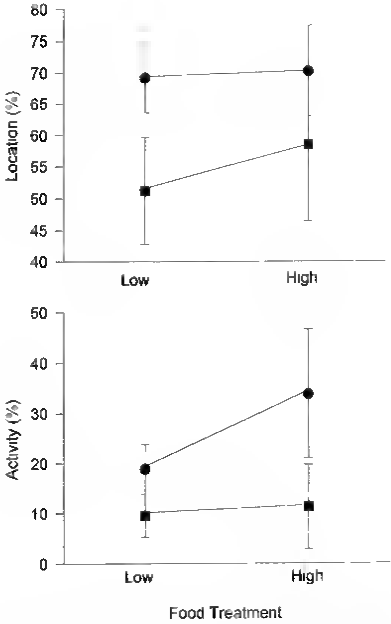

Figure 5-2. Mean (+ 1 SD) responses of Rana utricularia tadpoles to food level and predator treatments. Percentage of tadpole on the side of the container opposite the predator (top) and percentage of tadpoles that were active (bottom). Circles indicate predator absent and squares indicate predator present. (n=6 for all treatments)

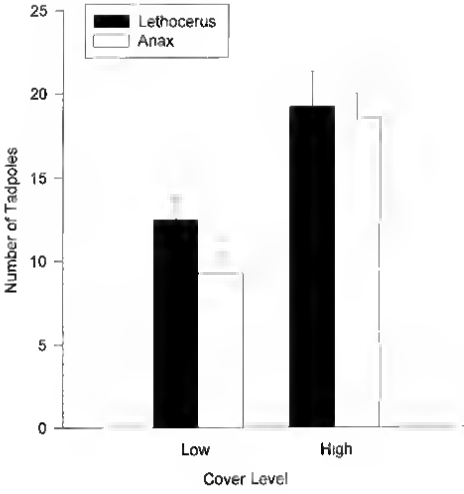

Figure 6-1 Number of Hyla squirella tadpoles that survived predation under different cover levels. Bars are means + 1 SE (n=4 for each bar)

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy

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Assistant Professor of
Wildlife Ecology and
Conservation

This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy

August, 1996

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Agriculture

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